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Pathogens for biological control of nematodes

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ABSTRACT. This review briefly examines some of the earlier research that lists the natural soil enemies of plant-parasitic nematodes. The major emphasis is on research developments of the past decade that consider biological control of nematodes. The importance of biocontrol has arisen as a consequence of the loss of the two effective but hazardous nematicidal soil fumigants, namely dibromo-chloropropane and ethylene dibromide, and because of the urgent need for new control strategies that their passing has created. Reports of successful biocontrol of plant nematodes by the fungal agents *Nematophthora gynophila*, *Dactylella oviparasitica* and *Paecilomyes lilacinus* and by the bacterial agent *Pasteuria penetrans* are examined. These recent developments are analysed and their implications on future research of nematode biocontrol discussed.

Introduction

Utilizing the natural enemies of pest nematodes as biological control agents of the nematode diseases of crop plants is certainly not a recent idea to nematologists. Nathan Cobb (1917), the pioneer of nematology in the US, specifically suggested that predacious nematodes might serve as biological control agents for the management of nematodes; how- nematologists such as Thorne (1927), Linford (1937), Drechsler (1941), Duddington (1962), Pramer (1964), Rodriguez-Kabana, Jordan and Hollis (1965), Mankau (1980), Kerry (1980a,b) and Stirling (1984), as well as others, have summarized investigations on the many soil micro-organisms antagonistic to nematodes. These reports have suggested methods for utilization of natural enemies as management tools of several plant-parasitic nematode diseases.

Fungal parasites of larvae

One group of natural enemies, the nematode-trapping fungi, has been investigated extensively (Table 1 and Figures 1, 2). Nearly all of these fungal species, which are facultative parasites, are easily cultured. Because they are non-specific parasites and not aggressive towards nematodes, their control of plant disease has been marginal and usually less than that obtained with nematicides. Consequently, trapping-fungi have not gained acceptance in the United States as reliable control agents for the management of nematodes; however, in France a commercial preparation of one isolate of *Arthrobotrys* sp. (Royale 300®) is sold for nematode control in mushroom culture and another *Arthrobotrys* sp. (Royale 350®) as a biological control agent against root-knot nematode problems on tomato (Cayrol, 1983).

Research on trapping fungi is not easily dismissed. These ubiquitous soil fungi are fascinating because of their unique morphology for ensnaring prey (i.e. sticky networks and constricting loops; Figures 1, 2). Much of the early research on biological control of nematodes was dominated by these forms and will probably continue because they may serve as research models of fungus–nematode interactions. To avoid a lengthy historical account of biological control of nematodes we need go back only 10 years to two unfolding situations that changed the direction and emphasis of the research programmes examining the soil enemies of nematodes. The first situation created the need to investigate alternatives to the popular chemical control methods. In 1977, two effective but hazardous

TABLE 1. Principal studies on biological control of nematodes by nematode-trapping fungi (Tribe, 1980)

Investigator	Year	Nematode	Location
Linford	1938–9	*Meloidogyne*	Hawaii
Deschiens	1941–3	*Meloidogyne*	Paris
Duddington	1956–61	*Heterodera*	England
Hams & Wilkin	1961	*Heterodera*	USSR
Soprunov	1958	*Meloidogyne*	USSR
Tarjan	1961	*Radopholus*	Florida, USA
Mankau	1961	*Meloidogyne*	California, USA
Cayrol & Frankowski	1978–present	*Ditylenchus* and *Aphelenchus; Meloidogyne*	France

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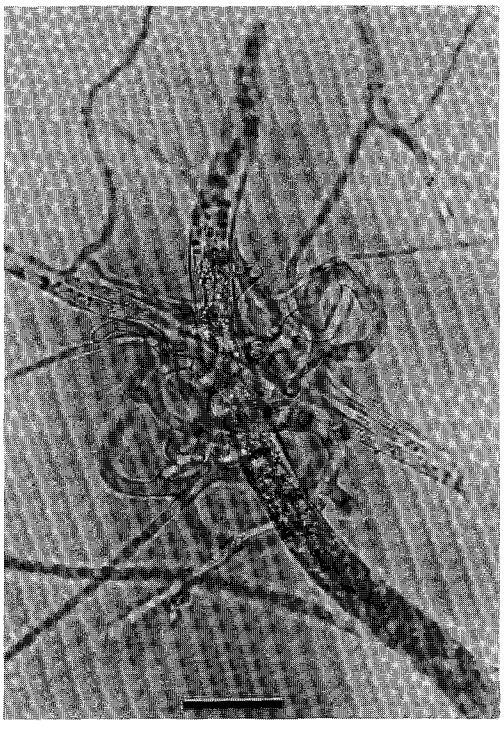

FIGURE 1. A nematode larva trapped in the sticky network of an *Arthrobotrys* sp. and colonized by the fungus. Bar = 30 μm.

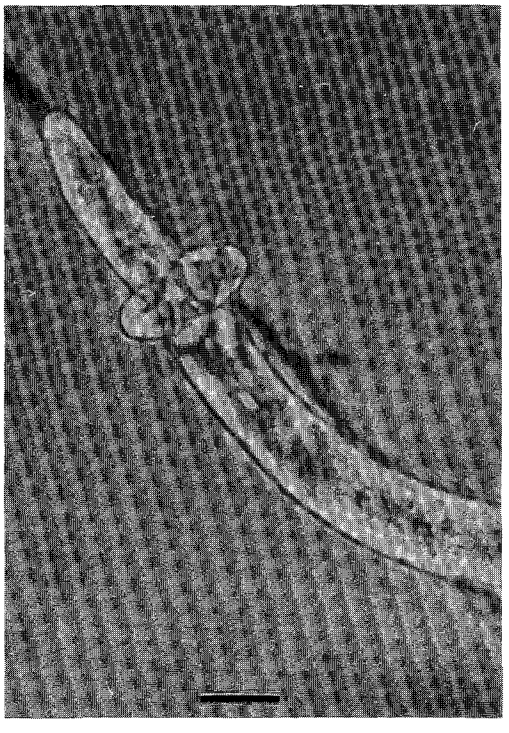

FIGURE 2. Larva ensnared by a constricting ring and colonized by an *Arthrobotrys* sp. Bar = 15 μm.

nematicides were banned: namely the DBCPs (1,2-dibromo-3-chloropropane) with the trade names of Fumazone® , Nemagon® and, more recently (in 1984) the ethylene dibromide soil fumigants designated Dowfume W-85® , and formulations of Soilbrom® . Their loss has placed severe constraints on control strategies for management of nematode pests (Table 2).

TABLE 2. Available registered broad-use nematicides (United States)

Use and common name*	Found in ground water	**Possibility of special review
Seed-bed and pre-planting soil fumigation		
Chloropicrin		
1,3-D (1,3-dichloropropene)	×	×
Metham		
Methyl bromide	×	×
Pre-planting, at planting and post-planting treatments		
Organophosphates		
Fensulfothion		
Ethoprop (ethoprophos)		
Phenamiphos (fenamiphos)		
Carbamates		
Carbofuran	×	×
Aldicarb	×	×
Oxamyl (systemic)	×	×

*IUPAC chemical names. Aldicarb: 2-methyl-2-(methylthio)propionaldehyde *O*-methylcarbamoyloxine; carbofuran: 2,3-dihydro-2,2-dimethyl-7-benzofuranyl methylcarbamate; chloropicrin: trichloronitromethane; 1,3-D: 1,3-dichloropropene; ethoprophos: *O*-ethyl *S*,*S*-dipropyl phosphorodithioate; fenamiphos: ethyl 4-methylthio-*m*-tolyl isopropylphosphoramidate; fensulfothion: *O*,*O*-diethyl *O*-4-methylsulphinylphenyl phosphorothioate; metham: methyldithiocarbamic acid; methyl bromide: bromomethane; oxamyl: *N*,*N*-dimethyl-2-methylcarbamoyloxyimino-2-(methylthio)acetamide.

**Future use of material in doubt pending review by Environmental Protection Agency.

Fungal parasites of eggs and adults

Fortunately, during this same period it was demonstrated that certain naturally occurring enemies of nematodes were effective biological suppressors of root-knot, cyst and other nematodes. These newly recognized nematode-destroying fungi were found parasitizing eggs and adult stages of nematodes. In his monograph in 1977, Barron (1977) considered only one species, *Rhopalomyces elegans* Corda, as an egg parasite. Currently, over 140 new fungal species have been identified which attack or have been associated with egg or adult stages of nematodes. This shift to explore new kinds of nematode parasites came about largely as the result of investigations in England on the cereal cyst nematode (CCN), *Heterodera avenae* Wollenweber. Gair, Mathias and Harvey (1969) and Williams (1969) observed that CCN occurred widely and yet, despite frequent or continual cropping of cereals, the numbers of nematodes remained relatively small and caused only minor yield losses. The explanation for this situation came from their research experiments where nematode-infested soils were treated with formalin solutions at fungicidal—not nematicidal—rates, resulting in the resurgence of the CCN populations. Williams (1969) concluded that a root-infecting fungus, *Gaeumannomyces* (*Ophiobolus*) *graminis* v. Arx and Olivier (the take-all disease pathogen), or other soil micro-organisms could be suppressing CCN populations. Kerry, Crump and Mullen (1980) continued investigation on nematode-suppressive soils of southern England, and demonstrated the presence of a few fungi that directly parasitized the CCN adult females and destroyed their eggs. The fungi *Nematophthora gynophila* Kerry and

Crump (Figure 3), *Catenaria auxillaris* (Kühn) Tribe (Figure 4), *Verticillium chlamydosporium* Goddard, and a lagenidiaceous species parasitized both the eggs and adults of CCN. In discussing his findings, Kerry (1980b) pointed out that the parasite's ability preferentially to attack and destroy adult females exerted great pressure on nematode populations by virtually destroying their reproductive capacity. The emerging adult females on cereal roots were parasitized by the motile zoospores of *N. gynophila* and were effectively controlled. The zoospores were able to move more readily in wet than dry soils. This increased activity and motility of the fungus in wet soils explained why the fungal parasite was a more effective control agent against the CCN in moist rather than drier soils (Kerry *et al.*, 1980).

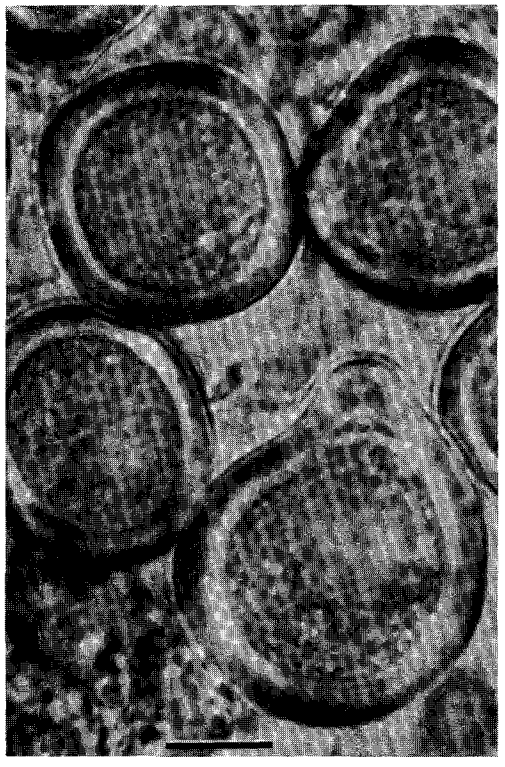

FIGURE 3. Resting thick-walled spores of *Nematophthora gynophila* coming from a parasitized cyst of *Heterodera avena*. Bar = 10 μm. (Photograph courtesy of B. R. Kerry).

Two additional investigations occurring during this period reinforced the idea that fungal parasites of the eggs and adults of nematodes functioned as effective biocontrol agents of nematodes. In California, Stirling and Mankau (1978) found a fungal species that attacked eggs and adults of *Meloidogyne javanica* (Treub) Chit. In peach orchards they observed that some soils were suppressive to nematode populations. They isolated and named a new fungal species, *Dactylella oviparasitica*, Stirling and Mankau, that attacked eggs and adults of the root-knot nematode. Later, they concluded that this fungus operated as a nematode biocontrol agent (Stirling, McKenry and Mankau, 1979).

Similarly, in South America, Jatala, Kaltenbach and Bocangel (1979) at the International Potato Center, Peru, found, isolated, and cultured a common soil-inhabiting fungus *Paecilomyces lilacinus* (Thom) Samson that parasitizes the eggs and adults of *M. incognita* and *Globodera pallida* (Stone) Behrens (Figure 5). When the fungus was cultured on grain, then added to field plots, it was sometimes effective against *M. incognita*. Currently, *P. lilacinus* is being

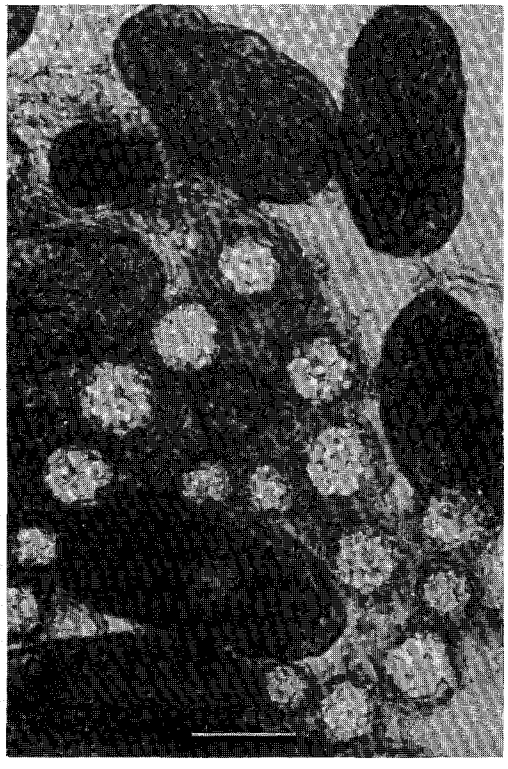

FIGURE 4. Several spherical reticulated spores of *Catenaria auxilaris* with a few eggs of *Heterodera glycines*. Bar = 10 μm.

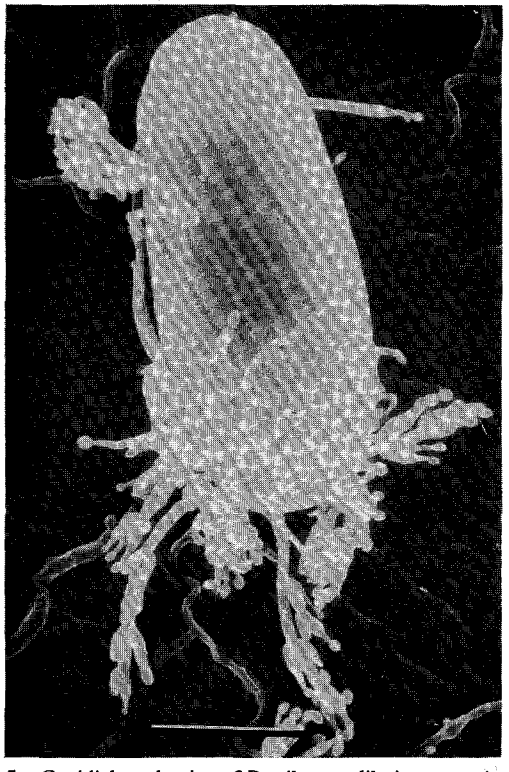

FIGURE 5. Conidial production of *Paecilomyces lilacinus* emerging from a colonized egg of *Meloidogyne incognita*. Bar = 10 μm.

tested in widely separated geographical areas by some participants in the International *Meloidogyne* project as a possible biological control agent of the root-knot nematode.

Recently, additional reports have found fungal parasites on the eggs and adults of nematodes. Fungal parasitism of the eggs of cyst-nematodes (genus: *Heterodera*) was analysed in depth by Tribe (1977). He listed *Verticillium chlamydosporium* Goddard and a 'contortion fungus' as the major pathogens and of lesser importance were *Cylindrocarpon destructans* (Zinssmeister) Scholten, a 'black yeast', and a 'crystal-forming fungus'. Other fungi associated with cysts were mycorrhizal fungi, *Pythium* spp., *Fusarium* spp., *Phoma* spp., *Penicillium* spp. and diverse *mycelia sterilia.* These fungi were considered weakly parasitic, because they were few in number and infrequent in occurrence.

From the above data a group of generic names emerge, suggesting that a mixture of soil-inhabiting and plant pathogenic fungi are also capable of parasitizing nematodes. Similarly, Dunn (1983) identified the fungus *Paecilomyces nostocoides* Dunn in *H. zeae* cysts (Figure 6). Again, a fungal genus considered to be a common soil inhabitant was found associated with nematode eggs. In addition, Godoy, Rodriguez-Kabana and Morgan-Jones (1982, 1983) and Morgan-Jones, Godoy and Rodriguez-Kabana (1981) have found a mixture of soil fungi and plant, insect and animal fungal pathogens, associated with the eggs of *M. incognita* and *M. arenaria.* In 1983, Clovis and Nolan (1983) found an array of fungi associated with the eggs of *Globodera* in Newfoundland. Of interest

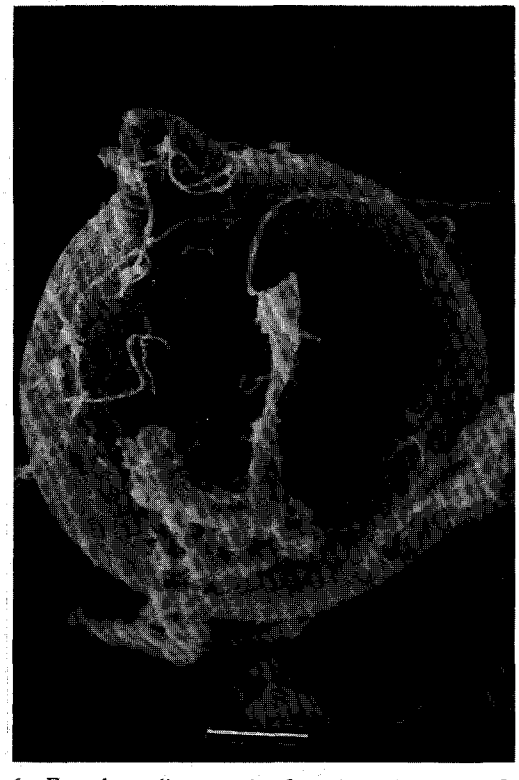

FIGURE 6. Fungal mycelium growing from the neck opening of a cyst of *Heterodera zeae.* Bar = 100 μm.

was the absence of *Verticillium* sp. from their list. Earlier, this common soil inhabitant was found to be a primary control agent operating against the CCN in England but failed to attack *Globodera.* Tribe (1980) suggested that morphological features of *Globodera* (i.e. reduced cyst apertures and extra cuticular layers) may have restricted parasitism by this fungus.

Another species of nematode surveyed for occurrence of fungi is the soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe. Morgan-Jones, Gintis and Rodriguez-Kabana (1981), Gintis, Morgan-Jones and Rodriguez-Kabana (1983) have surveyed several southern states (Arkansas, Missouri, Alabama and North Carolina) and have compiled a list of 51 fungal species associated with the eggs of the SCN. Again, a mixture of soil fungi and/or plant, insect and animal fungal pathogens was found. If the name of the host, SCN, were not known, a plant pathologist might conclude that these isolates were from diseased plant roots. These lists underline the obvious problem in selecting soil fungi as biocontrol agents of nematodes: many potential nematode control agents are also potential plant pathogens. Fungal parasites of animal and man also occur in the list; *Aureobasidium* sp. is one such species. This dual parasitism presents an additional selection problem—that of human safety in using soil fungi as biological control agents. Fungi can be opportunistic pathogens: if tissues of any organism are weakened or injured, some weakly pathogenic fungi might invade. For example, there have been several reports in the medical literature of keratitis in humans caused by *P. lilacinus* (Minogue *et al.*, 1984). Usually the organism has been isolated from eye tissue that was weakened by previous surgery (Pettit *et al.*, 1980). Although these reports cast doubt on the utilization of this particular fungus as a safe biocontrol agent, they do reaffirm the constant need for the diligent research and testing of any product for its public safety and impact on the environment.

Bacterial parasites

Bacterial insecticides (e.g. Doom® , Japidemic® and Milky Spore®) have been found useful in controlling soil insects. Numerous inherent similarities exist between soil insects and nematodes: these include their response to physical factors, some morphological and physiological characteristics, and their moulting. These similarities suggest that many of the principles of biocontrol used in entomology, with appropriate modifications, can be applied to control nematodes. Recently the bacterial pathogen of plant-parasitic nematodes, *Bacillus penetrans* (Mankau, 1975) was recognized, and compared favourably with the milky spore disease organism of insects, *B. popilliae* (Figures 7–10). As a consequence of several studies, the name *B. penetrans* was questioned by Sayre and Starr (1985), who proposed that the bacterium be designated *Pasteuria penetrans*, Sayre and Starr.

The life cycle of the bacterial endoparasite of *M.*

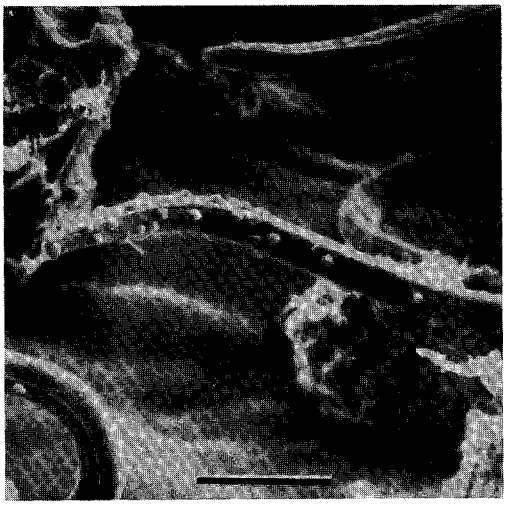

FIGURE 7. Numerous spores of *Pasteuria penetrans* attached to a few larvae of the root-knot nematode *Meloidogyne incognita*. Bar = 100 μm.

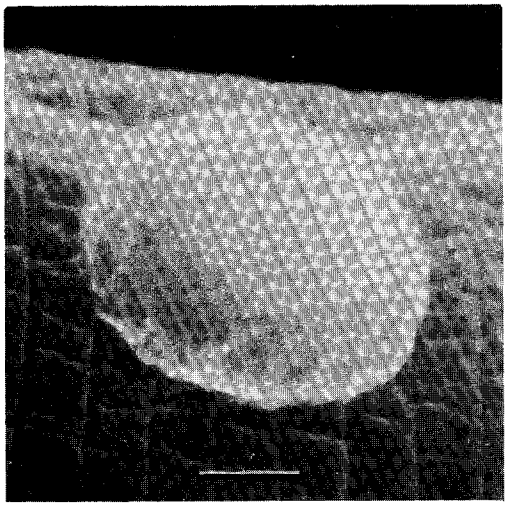

FIGURE 8. A spore of *Pasteuria penetrans* attached to the cuticular surface of a larva of *Meloidogyne incognita*. Bar = 1·0 μm.

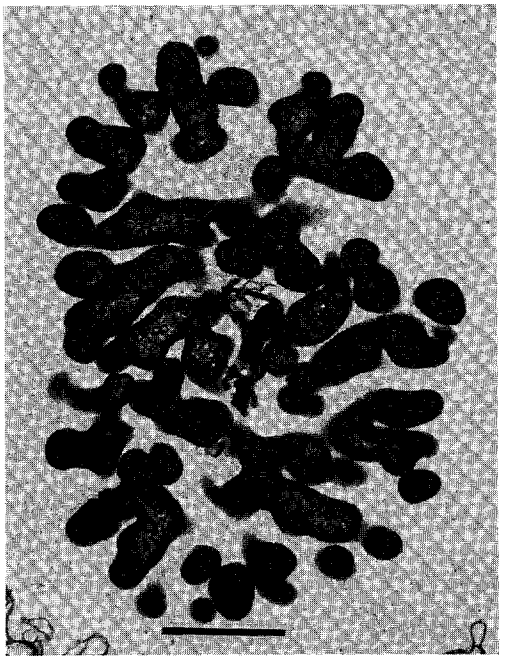

FIGURE 9. Cross section of a vegetative microcolony of the bacterium, *Pasteuria penetrans*. Bar = 2·0 μm.

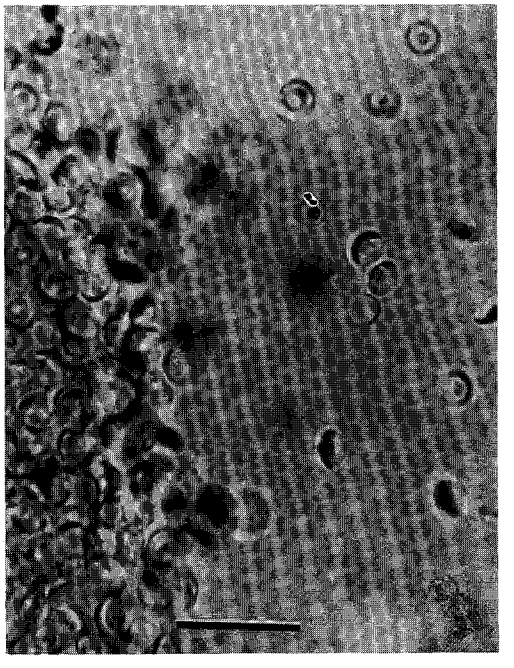

FIGURE 10. Numerous spores of *Pasteuria penetrans* floating out of a ruptured adult root-knot nematode. Bar = 10 μm.

incognita was examined by scanning and transmission electron-microscopic studies (Sayre and Wergin, 1977; Figures 7–10). The infective stage was initiated by attachment of endospores to the surface of a larva (Figures 7 and 8). A germ tube then penetrated the nematode cuticle and filamentous microcolonies of the bacterium formed in the pseudocoelum (Figure 9). Sporulation occurred when terminal cells in the microcolonies enlarged and formed sporangia. A septum within each sporangium divided the forespore from the basal or parasporal portion of the sporangium. The forespore within the sporangium was enclosed by several laminar coats. After the newly formed spores were released into soil (Figure 10), their sporangial coats were degraded, exposing the adhesive microfibres and enabling the free spores to attach to nematodes.

The discovery of the bacterial nature of the parasite encouraged the hope that the organism could readily be cultured and added to nematode-infested soil to serve as a natural nematicide (Mankau, 1975). Compatibility of the parasite with chemical nematicides was also established by Mankau and Prasad (1972). Spores of the parasite survived nematicidal dosages of Telone®, Nemagon®, Mocap®, Furadan® and Nemacur®, without losing their ability to attach to larvae and infect. These authors also found that the parasite was highly effective in reducing galling on tomato plants caused by *M. javanica* and *M. incognita*. *Pratylenchus scribneri* Steiner populations were reduced 53% in soil and 63% on plant roots, 55 days after spores of *P. penetrans* were added to nematode-infested soil in pot experiments. Prasad (1971) reported that his isolate of the bacterial

parasite exhibited distinct specificity on 16 nematode species tested, but only five species became infected. He also assembled a list of other nematode species reported to be a host of *P. penetrans*. Nematode taxonomists in the course of their systematic studies have illustrated and reported on the occurrence of the bacterium in several nematode species from widely separated areas throughout the world (Spaull, 1981).

In garden microplots Mankau (1973) tested the bacterium's ability to control root-knot nematodes using the following three treatments: (1) quantities of greenhouse air-dried soil infested with spores of the bacterium were used to fill holes 3 inches (≈76·2 mm) in diameter and 6 inches (≈152·4 mm) deep; (2) 1-month-old tomato seedlings infected with root-knot and parasitized by the bacterium were transplanted into the plots; and (3) 240 000 *M. incognita* larvae free of the bacterium were inoculated 4 inches (≈101·6 mm) deep into the soil. Each treatment was replicated 24 times. These microplots were planted to tomatoes and 11 months later samples were taken from nematode-infested areas and assayed by the addition of healthy larvae: 98% of the larvae from treatment 1 were encumbered with 20–50 spores, while 53% of the larvae from treatment 2 and only 7% of those from treatment 3 were found with the same number of spores. Thus, infested soil appeared to be an effective and more convenient method for introducing the parasite into the field than using tomato seedlings which harboured the bacterium and nematode.

In Australia, Stirling and Wachtel (1980) devised a method for the large-scale production of *P. penetrans* for field studies of the biological control of root-knot nematodes. Root systems of tomato plants containing large numbers of *Meloidogyne* females parasitized by *P. penetrans* were air-dried and finely ground to produce a powdery material which was light and easy to handle and store. These preparations of bacterial spores, when incorporated into a soil at a rate of 100 mg/kg, resulted in 99% of the nematode larvae being encumbered with the spore within 24 hours. Stirling (1984) also used these spore preparations in root-knot infested field soils at the rates of 212–260 mg/kg of soil, and found that root-galling and number of nematodes recovered at harvest time were significantly reduced. Significant economical control of root-knot nematodes was obtained in the fields when at least 80% of the bioassayed juveniles were encumbered with 10 or more spores per larva. They stated that the control was similar to that usually obtained with chemical nematicides.

Conclusion—possible lines of research

The primary goal of past and future research on the natural enemies of nematodes remains the development of feasible economic methods for the management of plant-parasitic nematode diseases. Although the numerous known antagonists of nematodes are certain indicators that biological control occurs naturally in soils, the sheer number of potential biocontrol organisms presents a formidable challenge to the few investigating nematologists. They must select from these few hundreds a workable investigative model that includes one or a few natural enemies virulent to one or more economically important nematodes in a particular agroecosystem. Some guidance in the selection of natural enemies is offered by Mankau (1981) and Kerr (1982, Table 3), who have listed favourable characteristics that antagonists should possess to function effectively as control agents of nematodes; to date, these characteristics have not been found in any one of the many enemies of nematodes.

Of the many soil organisms found associated with dead or dying plant nematodes, relatively few have been examined beyond their isolation in culture, identification and cataloguing. Most remain to be evaluated as possible bioregulators of nematode populations. Consequently, for nematologists, research opportunities are numerous, but resources are finite. Because of limited resources the following research goals are here selected for discussion: (1) investigations of the soil community or nematode habitat; (2) research efforts in the area of antagonist–nematode interactions; (3) the cellular studies leading to possible genetic manipulation of natural enemies to increase their nematicidal potential.

Investigations of the nematode's habitat

The habitat in which a natural enemy must function will determine its degree of success as a biocontrol agent. Efficacy of an antagonist must first be measured to determine if there is any margin for improving its potential as a parasite. One possible method for measuring and recognizing the influence of antagonists on nematodes might be through the construction of life tables. Orbach (1965) constructed such tables for *Ditylenchus triformis* Hirschmann and Sasser. Application of his technique to field studies should lead to the recognition of crashes in nematode populations, suppressive soils and possibly correlations of these observations with a particular parasite of nematodes.

Another method for measuring the efficacy of a nematode antagonist is through bioassay. The immediate problem with any bioassay is the development of standard procedures that are widely acceptable

TABLE 3. List of characteristics of an ideal biological control organism (after Kerr, 1982)

Able to survive in soil in active and inactive form.
High probability that organism contacts its host.
Multiplication in laboratory simple and inexpensive.
Amenable to packaging, distribution and application.
Should be specific for target organism.
Should not be a health hazard.
Active under appropriate environment.
Controls the target organism economically.

to all investigations. Standard bioassays could be utilized among several laboratories to select the more virulent or aggressive colonizers of nematodes. Bioassay will also provide information on the susceptibility of nematodes to a disease. This is an area of cooperation that should be jointly explored by a few laboratories.

Another approach to understanding the ecology of a habitat is through modelling or the computer programing of a nematode–parasite relationship. Currently, a few models simulating the host-plant–nematode relationships are available. Perry (1978) has gone an extra step beyond these programs and has incorporated in his model the effects of parasitic fungi on populations of the cereal cyst nematode. His model fits well to field data and correctly accounted for the increased rate of fungal infection in nematode populations with the increased amount of rainfall, especially in soils that were well drained. Future adjustment to this model, as well as others being developed, should improve our insight into the important edaphic factors governing soil habitat relationships.

Manipulation of soil microbial populations by addition of soil organic supplements has, more often than not, resulted in the reduction of damage caused by nematodes. Supplements are thought to initiate a succession of events favouring bacteria, microbivorous nematodes, nematode-trapping fungi and other soil antagonists over plant-parasitic nematodes. The succession of these organisms facilitates the stepwise degradation of soil organic matter. The numerous products released during this succession vary from complex to simple molecules that have toxic, antibiotic or inhibitory effects on plant-parasitic nematodes. The measurement of these products, through bioassay techniques and other means, presents a future research challenge that offers clues as to how natural biocontrol agents function in nematode-suppressive soils. There has not been a sustained effort to manipulate the soil environment and to use microbial processes in ways to manage pest-nematode populations, but there is sufficient knowledge to build upon.

Interactions of antagonistic nematodes

Fundamental information is needed on the interactions of nematode populations with their natural enemies. Specifically, there is a need to elucidate the communication systems and associated behavioural phenomena between important nematode species and their natural enemies. Knowledge of behaviour-modifying chemicals of nematodes and their fungal enemies is lacking. No communications systems have been identified, but semiochemicals similar to those recognized and found important in interactions of insect species are probably responsible for some fungus–nematode interactions. Several behaviour-modifying semiochemicals from insects have been isolated, identified and synthesized (Nordlund, Jones and Lewis, 1981). The strategies employed by fungal pathogens to seek out and parasitize nematode hosts are probably similar to those insect–host systems.

The fungus–nematode interaction can also be influenced by certain environmental changes that stress the physiology of the nematode. Van Gundy *et al.* (1962) suggested the possibility that nematodes may be made susceptible to parasites when they have been weakened by low oxygen concentrations. Sayre and Keeley (1969) suggested that nematodes in a very dilute suspension of a medium were more susceptible to attack from the fungus, *Catenaria anguillulae* Sorokin, because of the osmotic stress and, in this situation, their excretory products were more abundant and attractive to zoospores of the fungus. Technologies are available and amenable to studies on the behaviour of nematodes and their natural enemies.

Genetic manipulation

Fundamental information is needed at the cellular level to allow for a better understanding of how to select and genetically manipulate biocontrol agents of nematodes. The information would underpin possible genetic modifications of the hyperparasites of nematodes and their management in soil.

Already, a backlog exists of some 140 species of fungi suspected of being possible antagonists and biocontrol agents of nematodes. The selection and evaluation of the more virulent isolates of these fungi represents a substantial future research commitment. For each isolate an *in vitro* culture technique must be found and a bioassay devised using Koch's postulate that would determine the pathogenicity of the fungus to the nematode. In addition, a need exists to develop physiological information on each isolate to determine, for example, if the production of chitinolytic enzymes, that may promote nematode colonization and serve as markers for promising biological control agents of nematodes, is possible. There have been recent advances in genetic manipulation and strain improvements for filamentous fungi in industrial and medical research (Ball, 1980). Technologies have been developed to improve end-product production in filamentous fungi (e.g. from amino acids to secondary macromolecules such as enzymes) (Johnston, 1975). These developed technologies can be used to study the genome modification of parasitic fungi of nematodes. However, very little is known about these fungi and knowledge must be acquired on how to isolate genes, modify their structures and determine how the genes that are responsible for biocontrol and other desirable characters are expressed. Strain improvement in *Aspergillus* species has resulted from selection techniques and use of natural genetic variation (Johnston, 1975). Chemical selection agents have also been used to increase enzyme output. Many of these selection techniques may be suitable for strain improvement in the nematode-destroying fungi, but understanding nuclear determination and stability are important.

The research outlined above is intended to centre

mainly on the newly recognized nematode antagonists that appear to be successful biocontrol agents, and to consider their habitat, interactions and possible genetic manipulation. These efforts are in line with those of N. A. Cobb (1917), the pioneer nematologist who first envisaged biocontrol of nematodes. He offered this advice which is still valid today:

> The soil is the habitation of a vast community of beings with all the attributes of other huge agglomerations of living things having varying needs, instincts and aspirations; and it is just as inappropriate to look upon it as inorganic as it would be to look upon a great city as merely an agglomeration of hills, streets and houses. Here in the soil are beings in enormous variety; multiplying, growing, dying; competing, fighting, cooperating one with another, with an activity almost if not quite defying the imagination, and we need what may be called soil biologists or geobiologists, who shall understand, as far as possible, this interplay of life forces that gives us food, fiber and fuel. To a considerable degree our progress in agricultural knowledge in the not distant future will be in proportion to the firmness with which we lay hold of and act on this idea.

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